

**PREY CHOICE BY *NESTICODES RUFIPES*
(ARANEAE, THERIDIIDAE) ON *MUSCA DOMESTICA*
(DIPTERA, MUSCIDAE) AND *DERMESTES ATER*
(COLEOPTERA, DERMESTIDAE)**

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ABSTRACT. *Nesticodes rufipes* is widely distributed in tropical and subtropical regions, being strongly associated with humans. However, few behavioral and ecological studies have investigated interspecific interactions between these spiders and insects of medical and veterinary importance. Here, we have investigated prey choice by *N. rufipes* when two different prey species, *Musca domestica* and *Dermestes ater*, were offered simultaneously. We also quantified the capture of these prey types by this predator in a poultry house and analyzed the association between prey-choice with physical characteristics of the prey. Finally, we discuss whether there is an antagonistic intraguild interaction in such a system composed of *N. rufipes* (top predator), *D. ater* (predator of larvae of *M. domestica* and prey of *N. rufipes*) and *M. domestica* (*N. rufipes*' prey). We found that *Musca domestica* were more abundant than *D. ater* in *N. rufipes* webs in the poultry house. Spiders given a choice of adults of *M. domestica* plus adults of *D. ater*, and also on adults plus larvae of *M. domestica*, preyed more on adult flies than on the other prey types. This preference was probably associated with the lesser mass and shorter lengths of adult flies. Our experiments demonstrated that the predation impact of *N. rufipes* on *D. ater* is low when compared to *M. domestica*. This result provides evidence that an antagonistic interaction between these predators does not occur, suggesting that they are in fact acting either synergistically or additively on *M. domestica* prey.

Keywords: Prey selection, housefly, spider predation, poultry house

Many spiders eat a wide variety of prey species (usually insects), and they usually present a sedentary foraging behavior (Wise 1993), suggesting that selection for habitat, not for prey, should be the rule. However, several prey capture specializations can be seen (Greenstone 1979; Riechert & Luczak 1982; Uetz 1992; Alderweireldt 1994; Onkonbury & Formanowicz 1997; Nyffeler 1999; Toft 1999), and some may have been an important influence on the evolution of insect defense behavior (Uetz 1990). It has been recognized that the choice of habitat (patch) in spiders is of primary importance through its effect on feeding rates, growth and reproduction (Riechert 1981; Morse & Stephens 1996). Nevertheless, once in a feeding patch, spiders typically are confronted with an array of potential prey species. Indiscriminate feeding is not advantageous because prey vary enormously in quality due to toxicity or nutrient content. Thus, active prey selection by spiders serves to find the optimal compromise be-

tween three "nutritional goals": to maximize energy intake, to balance nutrient composition of the body, and to minimize toxin consumption (Toft 1999).

Prey selection has been defined by Hassell (1978) as follows: "Preference for a particular prey is normally measured in terms of the deviation of the proportion of that prey attacked from the proportion available in the environment." A common form of prey specialization shown by spiders is on prey size (Uetz 1992), evidenced by some studies comparing the prey of spiders to that available in the environment (Uetz & Hartssock 1987; Uetz 1990).

Spiders are major components of the generalist predator guild that characterizes intermediate trophic levels in many terrestrial systems (Moulder & Reichle 1972; Manley et al. 1976; Spiller & Schoener 1996). Theory suggests that prey suppression by multiple predator species can lead to a variety of outcomes depending on the nature of the predator-predator interaction. Predator effects can be en-

hanced when predators interact either additively or synergistically (Finke & Denno 2002). Antagonistic interactions, on the other hand, result in diminished prey suppression, either because one predator disrupts the foraging behavior of another predator (Moran et al. 1996), or consumes the other predator (Polis & Holt 1992; Rosenheim 1998; Wise & Chen 1999).

Nesticodes rufipes (Lucas 1846) (Araneae, Theridiidae) (referred to as *Theridion rufipes* in references) is widely distributed in tropical and subtropical regions, extending to temperate zones, and these spiders construct irregular webs with a disordered aspect (González 1989). Its exact distribution is not easy to determine, since it is strongly associated with humans (Downes 1988; González & Estévez 1988; González 1989). Behavioral and ecological studies considering predation by *N. rufipes* are scarce. Fox (1998) highlighted the strategic importance of these spiders to the natural control of *Aedes aegypti* (Diptera, Culicidae), since the spiders incorporate a paralyzing substance in the webs, which paralyze the mosquitoes through contact, increasing their capture efficiency. Barreto et al. (1987) also mentioned the importance of *N. rufipes* as predators of *Rhodnius prolixus* (Hemiptera, Reduviidae).

Musca domestica (Linnaeus 1758) (Diptera, Muscidae) has a cosmopolitan distribution and high synanthropic indices (Smith 1986; Ferreira & Lacerda 1993), being also of considerable medical and veterinary importance (Harwood & James 1979; Smith 1986; Levine & Levine 1991). This species lives in human dwellings, poultry houses, supermarkets and garbage, growing on a wide variety of substrates such as food and vertebrate excrement (Axtell & Arends 1990; Bowman 1995). Although there are some chemical techniques aimed to control *M. domestica* in poultry houses, the negligent human behavior related to the correct application of chemicals has intensified the search for potential natural enemies of houseflies in order to diminish chemical applications (Cunha & Lomônaco 1996). Therefore, the understanding of the strength of interspecific interactions between *M. domestica* and its predators is of major importance.

Dermestes beetles grow in organic matter, such as carrion and dung that accumulate in

poultry houses (Cloud & Collison 1986). *Dermestes ater* (DeGeer 1774) (Coleoptera, Dermestidae) feeds and scavenges on animal products. However, sometimes it feeds on other insects, thus acting as a predator (Veer et al. 1996). For example, *D. ater* causes serious economic damage to sericulture, because the beetles feed on high numbers of *Bombyx mori* (Lepidoptera, Bombycidae) (Kumar et al. 1988; Bai & Mahadevappa 1996).

According to Lomônaco & Prado (1994), *M. domestica* (91.82%) and *Chrysomya putoria* (Diptera: Calliphoridae) (6.47%) were the most abundant fly species sampled in a poultry house located in the city of Uberlândia (MG), Brazil. These authors also observed that *D. ater* was one of the most frequent natural enemies of larvae and pupae of *M. domestica* in that system. As *M. domestica* (adults) and *D. ater* (adults and larvae) are usually seen in *N. rufipes* webs in poultry houses, and *D. ater* attacks and feeds on *M. domestica*, it is of major importance to understand the strength of interspecific interactions among these animals in such a system.

Here, we investigated prey choice by *N. rufipes* when two different prey species, *D. ater* and *M. domestica*, were provided at the same time as primary food sources. We also quantified the capture of these prey species by this predator in a poultry house, comparing the results with the prey choice experiment. Correlations of prey choice with physical characteristics of prey types are also presented. Finally, we discuss whether there is evidence of antagonistic intraguild interactions in such a system composed of *N. rufipes* (top predator), *D. ater* (intermediate predator and prey of *N. rufipes*), and *M. domestica* (*N. rufipes*' prey).

METHODS

Field observations.—An experimental poultry house located in the city of Botucatu-SP (Brazil) (22°52'20"S; 48°26'37"W) was chosen to collect insects captured by *N. rufipes* webs. From September 2001 to August 2002, all poultry house parts (walls, door crevices, wood supports, chicken cages, etc.) were examined monthly. When a web site containing *N. rufipes* was found, all arthropod carcasses caught in the web were removed and put into small glass tubes for identification. Spiders were never removed from their web

sites in order not to diminish their abundance, and we did not distinguish males from females, or even spiderlings from adults, that were inhabiting the webs. The carcasses were then taken to the laboratory where prey were identified. We recorded from each web the species of prey and also the respective month of collection. Voucher specimens (spiders and insects) from this study are deposited in the Invertebrate Collection of the Department of Parasitology, Unesp (Botucatu-SP), Brazil.

We compared which prey species were captured throughout the year by plotting the total number of flies and beetles (adults + larvae) captured monthly. In the same plot, we included the number of web sites observed by month.

Rearing of prey species.—While visiting the poultry house, we collected larvae of houseflies and adults of *D. ater* from small samples of chicken feces deposited below the cages and put them into small glass tubes. All insects were then taken to the laboratory where larvae of *M. domestica* were reared in vials containing wet ground animal ration (25 °C under 12 h light). After pupation, vials were kept in cages of nylon mesh on a wood frame (30 cm × 30 cm × 30 cm) where water and sugar were provided for adults. Adults of *D. ater* were kept in plastic boxes (15 cm × 45 cm × 30 cm) (25 °C under 12 h light) with large pieces of cotton which allows females to lay their eggs. Wet cotton and fish (sardines) were added weekly as water and food sources, respectively.

Prey choice.—Forty-five adult females of *N. rufipes* were captured in several buildings located on the campus of the University of the State of São Paulo (Botucatu, Brazil) from January–March 2003, and kept individually in clear plastic containers [10.5 cm × 11.5 cm (900 ml)] in the laboratory (25 °C under 12 h light). All spiders were of similar size range (15 mm). Before the prey choice experiments were carried out, a nylon mesh (10 cm × 3 cm) was internally fixed in each container in order to allow spiders to build their webs. All spiders were fed with both houseflies and dermestid beetles for a month (insects were randomly offered twice a week) in order to attain similar nutritional status.

After twenty-four hours of food deprivation (sufficient time for spiders to build their webs), fifteen containers with spiders received

five larvae (third instar) and five adults of *M. domestica* each. Another fifteen containers received five larvae (fifth instar) of *D. ater* and five adults of *M. domestica* each, and the remaining containers received five adults of *D. ater* and five adults of *M. domestica* each.

Before adding the different prey types into the spider containers, flies were immobilized by chilling in a freezer for three minutes. After that, flies were removed and put in a Petri dish together with the other insects [*D. ater* (larvae or adult) or larvae of *M. domestica*] previously removed from their laboratory rearing cages. When flies began to move, all ten insects were carefully dropped in the bottom of a spider container, without touching the spider web. This procedure prevented flies from being captured quickly due to their superior flying ability and it insured that flies could be easily separated prior to the experiments. In the first two minutes (approximately) inside the spider containers, flies just walked and then started flying. Prey consumption evaluation started twenty-four hours following the introduction of the insects.

The number of prey eaten by spiders was recorded according to the combination of prey types, and an analysis of variance (ANOVA) (Zar 1999) was computed comparing the mean proportions [$\arcsin(\sqrt{\text{proportion}})$] of adults of *M. domestica* consumed, since it was common for all combinations of prey. A Least Significant Difference test (LSD) was computed comparing the pairs of transformed mean proportions of adults of *M. domestica* consumed between the different prey combination treatments (adults + larvae of *M. domestica*, adults of *M. domestica* + larvae of *D. ater*, and adults of *M. domestica* + adults of *D. ater*). To test the hypothesis that prey choice was random, we compared the measured proportion of prey captured to the probability that prey capture was random (i.e. 50% chance of capturing house flies). We did this by constructing *t*-tests on the arcsin ($\sqrt{\text{proportion}}$) transformed data, which compared the mean transformed value to arcsin ($\sqrt{0.5}$).

Size of prey.—After the prey-choice experiments, many larvae (fifth instar) and adults of *D. ater* as well as larvae (third instar) and adults of *M. domestica* were randomly removed from their respective rearing cages

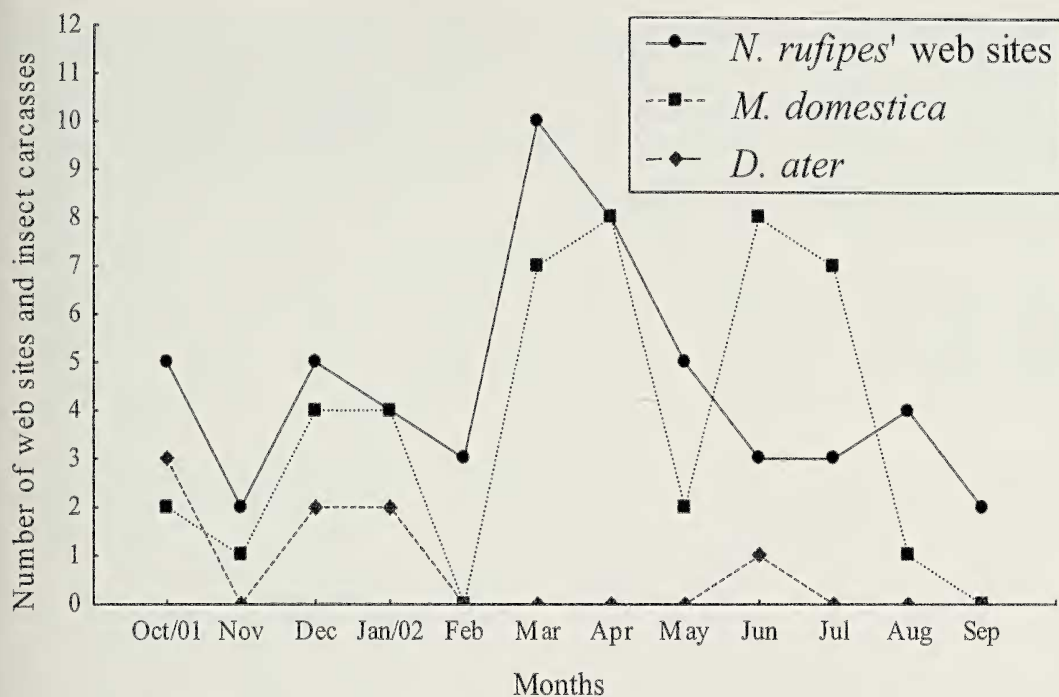


Figure 1.—Number of *M. domestica* (adults) and *D. ater* (adults plus larvae) carcasses collected from October 2001 to September 2002 in a poultry house located in Botucatu (SP), Brazil. The number of web sites observed is also included.

and, from there, twenty insects from each prey type were again randomly removed. These insects were first killed with ether solution (90%) and then measured (body length measured from anus to head without measuring wings for adult flies) by using a graduated micrometric ocular coupled to a stereoscopic microscopy and weighed with a semi-analytical scale. Student's *t*-tests were computed comparing pairs of mean weights and lengths for each combination of prey types. Thus, we tested whether the lighter and shorter prey were also the more preferable ones.

RESULTS

Musca domestica carcasses were much more abundant than *D. ater* (adults + larvae) on *N. rufipes* webs for most of the 12 months of collection (Fig. 1). The spiders in the poultry house ate more 5.5 times as many flies ($n = 44$) than dermestid beetles ($n = 8$) over the course of the year-long study (Fig. 1). Spiders captured a total of sixteen species of prey. Insects from orders Coleoptera (48.36%) and Diptera (34.02%) represented 82.38% of all prey captured, and for all months sampled *M.*

domestica was predominant as prey, since it represented 24.59% of the insects captured, followed by the coleopterans *Alphitobius diaperinus* (Tenebrionidae) (20.90%), *Aphodius* (Scarabaeidae) (10.25%), *Gnathocerus* (Tenebrionidae) (6.15%), and *D. ater* (3.28%). All dipterans except *M. domestica* represented only 9.4% of prey. Even though several prey were captured, in figure 1 we present data only related with the arthropod species studied here.

In the prey choice experiments, the number of adult flies consumed by spiders was significantly different when different combinations of prey types were offered ($df = 2$; $MS = 0.808$; $F = 4.185$; $P = 0.023$), and the combination of adults of *M. domestica* plus adults of *D. ater* showed the highest average proportion of adult flies consumed (Table 1).

The Student's *t*-tests showed that when spiders were placed in cages with adults of *M. domestica* plus adults of *D. ater*, or with adults of *M. domestica* plus larvae of *M. domestica*, spiders were selective and took more adult flies than the other prey (Table 1). Although the combination of adults of *M. do-*

Table 1.—Mean proportion of spiders that fed on adults of *M. domestica* given different combinations of potential prey. Student's *t*-tests were used to test for significance of difference using the transformed mean proportions [$\arcsin(\sqrt{\text{proportion}})$] of adults of *M. domestica* consumed and the probability of 50% [$\arcsin(\sqrt{0.5})$] of consumption. *Significant at $P < 0.01$. In addition, proportions followed by different letters differed statistically from each other [Least Significant Difference (LSD) test] at $P < 0.05$. *n* = Number of observations for each group. *n* = 14 and *n* = 13 means that one and two spiders did not feed on any prey during experimentation, respectively.

Combination of prey types	Mean proportion (\pm SD)	<i>n</i>	<i>t</i>	<i>P</i>
Adults \times Larvae of <i>M. domestica</i>	0.73 \pm 0.44 a	13	3.45	0.002*
Adults of <i>M. domestica</i> \times Larvae of <i>D. ater</i>	0.71 \pm 0.80 a	15	1.86	0.074
Adults of <i>M. domestica</i> \times Adults of <i>D. ater</i>	0.96 \pm 0.26 b	14	13.0	0.000*

mestica plus larvae of *D. ater* presented a nonsignificant result for adult flies consumed ($P = 0.074$), a strong tendency of spiders to consume more flies was evidenced (Table 1).

Adults of *M. domestica* weighed less when compared to the other prey offered to spiders, and it also had smaller body size since Student's *t*-tests were significant for all comparisons in all combinations of prey (Figs. 2, 3).

DISCUSSION

The preference of *N. rufipes* for adults of *M. domestica* might be associated with their

smaller mass and shorter lengths, probably because it would facilitate their being killed and handled by spiders. Prey activity would also explain why spiders captured disproportionately more adults of *M. domestica* than the other prey types (Table 1). According to Provancher & Coderre (1987), prey activity is believed to influence functional responses and switching of spiders for some prey. Although all prey species were highly active in the experimental containers, only adults of *M. domestica* could do a three-dimensional exploration in the container, since it flew over all

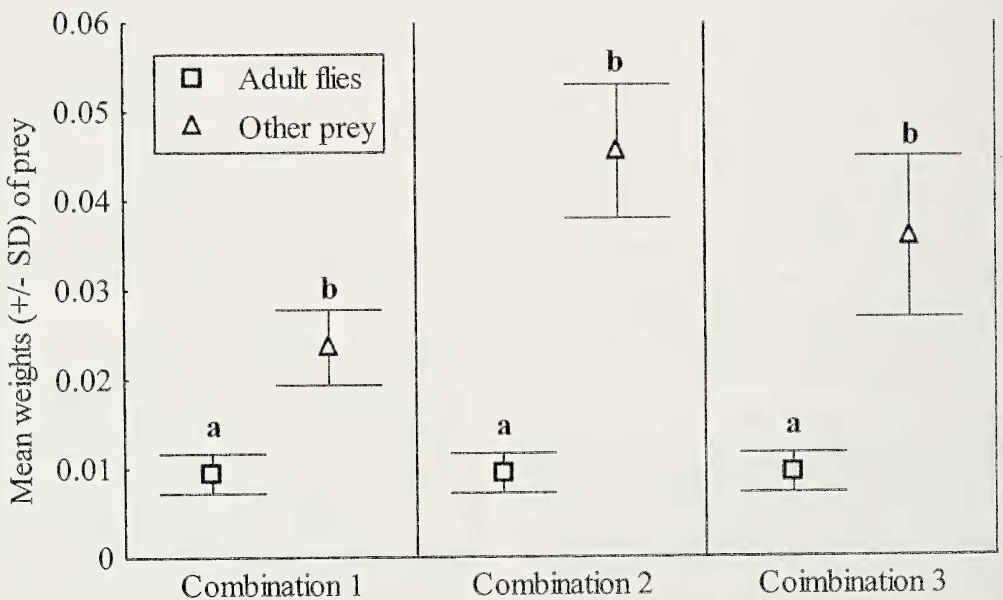


Figure 2.—Comparisons of mean weights (grams) of prey according to different combinations of prey types. A Student's *t*-test was computed for each combination and all analyses were statistically significant (All analyses had *n* = 20 and 38 degrees of freedom). Combination 1: adults + larvae of *M. domestica* (*t*-value = -13.27 ; $P < 0.01$); Combination 2: adults of *M. domestica* + larvae of *D. ater* (*t*-value = -20.60 ; $P < 0.01$); Combination 3: adults of *M. domestica* + adults of *D. ater* (*t*-value = -12.69 ; $P < 0.01$).

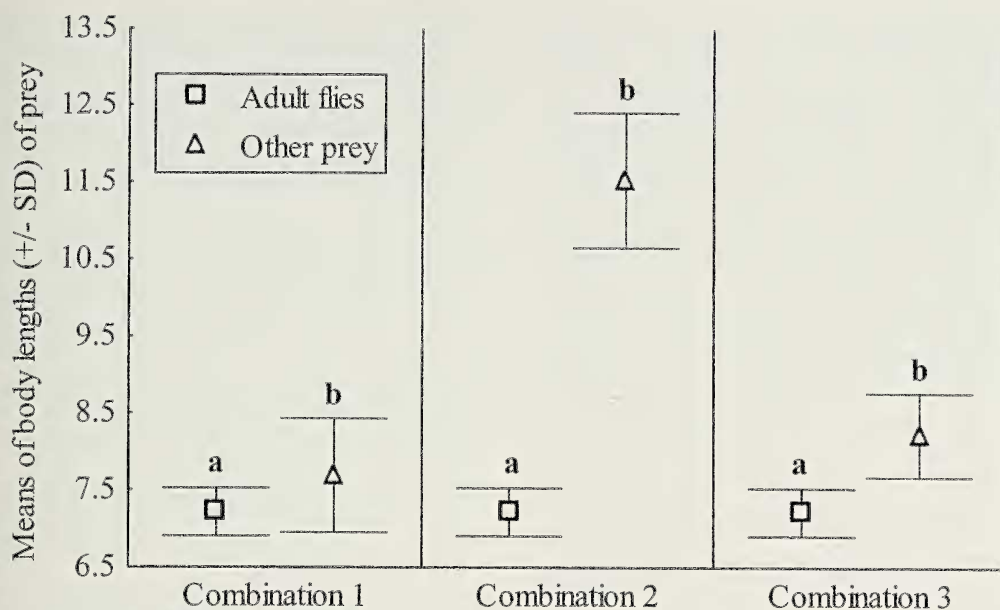


Figure 3.—Comparisons of mean lengths (mm) of prey according to different combinations of prey types. A Student's *t*-test was computed for each combination and all analyses were statistically significant (All analyses had $n = 20$ and 38 degrees of freedom). Combination 1: adults + larvae of *M. domestica* (t -value = -2.65 ; $P < 0.05$); Combination 2: adults of *M. domestica* + larvae of *D. ater* (t -value = -20.71 ; $P < 0.01$); Combination 3: adults of *M. domestica* + adults of *D. ater* (t -value = -7.15 ; $P < 0.01$).

areas of the container, probably increasing its frequencies of encountering the predator. The other prey types only walked intensively in the bottom of the container with the exception of adults of *D. ater*, which occasionally flew. The higher rate of consumption of adults of *M. domestica* when this prey was offered concomitantly with adults of *D. ater* (Table 1) is possibly associated with the rigidity of beetle exoskeletons, which may increase their rate of escape from spider attacks.

We observed that all spiders actively captured their prey rather than passively waiting for prey to fall randomly in their webs (sit-and-wait strategy). This behavior was possible because the available time given to spiders to build their webs (24 hours) was insufficient to enable them to weave large and dense webs. Large webs would allow spiders to catch prey only by a prey-web contact. Hence, the way that we set up the experiments ensured that webs were just used by spiders to increase their area of attack, forcing them to actively choose a prey type. It is important to state that all spiders wove webs in all parts of the containers, including the bottom, enabling them to capture all prey available. Thus, we con-

clude that preference of spiders for housefly adults was determined by prey behavior and physical characteristics of prey (length and weight) in addition to active spider prey choice.

Finke & Denno (2002) studied the combined impact of two salt-marsh-inhabiting invertebrate predators, the mirid *Tytthus vagus* (Heteroptera, Miridae) and the wolf spider *Pardosa littoralis* Banks 1896 (Araneae, Lycosidae), on suppression of their shared prey, the planthopper *Prokelisia dolus* (Hemiptera, Delphacidae), in simple and complex habitats. They observed that in simple habitats, the predators interacted antagonistically, due to intraguild predation of mirids by spiders, and predation pressure on the planthopper population was relaxed. However, for structurally complex habitats this antagonistic interaction was dampened by providing a refuge for mirids from spider predation. Our experiments demonstrated that the predation impact of *N. rufipes* on *D. ater* is low when compared to that on *M. domestica* (Fig. 1), and it provides some evidence that an antagonistic interaction between these predators (and scavenger) may not occur, suggesting that they are in fact act-

ing either synergistically or additively on *M. domestica* prey.

Considering that more than a hundred of pathogens are associated with *M. domestica*, such as those causing typhoid fever, cholera, tuberculosis, parasitic helminthiasis and protozoosis (Harwood & James 1979; Smith 1986; Levine & Levine 1991; Chavasse et al. 1999; Fischer 1999), synergistic and additive interactions between *D. ater* and *N. rufipes* have important practical implications since it may increase the likelihood of a natural suppression of housefly populations established in poultry houses. However, functional response studies of *D. ater* and *N. rufipes* on larvae and adults of *M. domestica*, respectively, are encouraged in order to understand the actual contribution of these predators in diminishing natural or experimental housefly populations.

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